

THE CRANIAL MORPHOLOGY OF THE FOSSIL BEAVER *DIPOIDES SMITHI* (RODENTIA: MAMMALIA)

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ABSTRACT. The cranial morphology of the genus of fossil beaver, *Dipoides*, has never been described or compared with that of other fossil and extant beavers. An extremely well-preserved skull recovered from north-central Oregon in 1974 allows for identification of nearly all features of the cranium. Variation in skull morphology in rodents is generally recognizable at the generic level, and intra-specific variation is usually reflected in differences in the dentition. The skull of *Dipoides* closely resembles that of *Eucastor* and *Castoroides* and differs noticeably from that of *Castor*. The regions of the skull with similarities to *Dipoides*, *Eucastor*, and *Castoroides* are (1) the bones of the lacrimal region; (2) the arrangement of foramina in the basicranium and interorbital region; and (3) the development of the alisphenoid wing of the internal pterygoid fossa. *Castor* differs in these three areas. Close examination of the crania of these four genera confirms that *Eucastor*, *Dipoides*, and *Castoroides* represent one group of beavers that has been phylogenetically distinct from that leading to the extant beaver, *Castor*, since the early Miocene.

INTRODUCTION

Species in the genus *Dipoides* Jäger, 1835, are small beavers that lived during the Hemphillian Mammal Age in North America. The genus appears to have evolved from *Eucastor* Leidy, 1858, during the late Miocene, approximately 8.5 mya (Wagner, 1981).

The genus *Dipoides* was first described by G.F. Jäger in 1835 from late Miocene deposits of Germany. Subsequently, other species of *Dipoides* have been described from late Miocene deposits of Eurasia and North America. R.A. Stirton (1935) reviewed the Tertiary beavers, presenting a phylogeny based on dental characters, with *Dipoides* in the lineage leading to *Castoroides* Foster, 1838. Later, Olson (1940) undertook a comparative study of the cranial foramina of the Castoridae. He described and compared the cranial foramina of *Paleocastor* Leidy, 1869, *Eucastor*, *Castoroides*, and *Castor* Linnaeus, 1758, noting evolutionary trends in foramina within the Castoridae. *Dipoides* was not included in that study.

J.A. Shotwell (1955) reviewed the genus *Dipoides*, basing his taxonomic conclusions on the dental morphology, pri-

marily P₄. He concluded with the description of a new species, *D. smithi* Shotwell, 1955, from McKay Reservoir in north-central Oregon. Stirton (1965) described the cranial morphology of *Castoroides ohioensis* Foster, 1838, in detail, increasing the knowledge of this giant castorid. The specimen of *D. smithi* that I describe in the present paper was recovered from the type locality of the species at McKay Reservoir (Fig. 1) in 1974 and provides new evidence concerning the cranial morphology of the genus and helps clarify its relationship to other genera of castorids.

METHODS AND MATERIALS

The abbreviations used in the text and tables are CNHM (Chicago Natural History Museum), UO (University of Oregon), and UCMP (University of California Museum of Paleontology). All measurements are in millimeters. The comparative specimens are:

Eucastor cf. *E. tortus* Leidy, 1858, CNHM P15787, Big Springs Canyon local fauna, Bennett County, South Dakota, Ogallala Group, Clarendonian.

Castoroides ohioensis Foster, 1838, CNHM P3800, Gravel Pit near Bellflower, McClean County, Illinois Pleistocene.

Castor canadensis Kuhl, 1820, UCMP 126-158, South Dakota, Recent.

Dipoides smithi Shotwell, 1955, UCMP 113422, McKay Reservoir local fauna, Umatilla County, Oregon, ? Shuttler Formation, Hemphillian (Figs. 2, 3 and 4).

SYSTEMATICS

Family Castoridae Gray, 1921

Subfamily Castoroidinae Trouessant, 1888

Genus *Dipoides* Jäger, 1835

Dipoides smithi Shotwell, 1955

Figures 2, 3, and 4

REFERRED MATERIAL. UCMP 113422, nearly complete skull lacking only the projection of the premaxillaries

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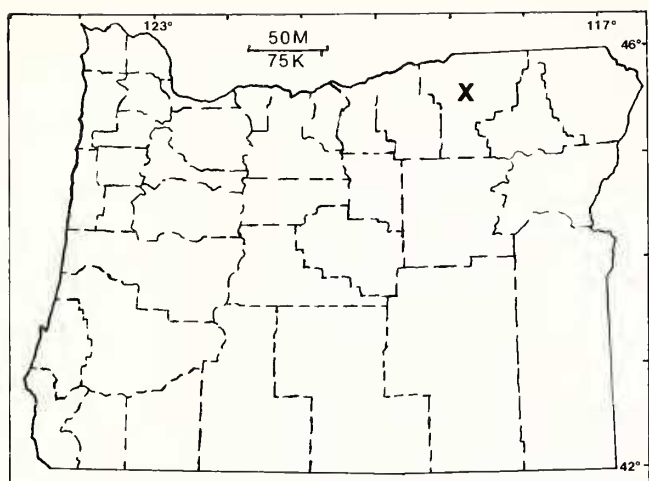


Figure 1. The skull of *Dipoides smithi* was recovered from UCMP locality V74163 at McKay Reservoir in Umatilla County in north-central Oregon, designated by an X.

and incisors (Figs. 2 and 3); UCMP 113433, left dentary fragment with P_4 , M_{1-2} (Fig. 4), both from locality UCMP V74163 = U02222, McKay Reservoir, Umatilla County, Oregon, ? Shutler Formation, Hemphillian.

DESCRIPTION AND COMPARISON. The dental morphology of UCMP 113422 agrees with the diagnosis of *D. smithi* (Shotwell, 1955). Upper molars and premolars lack parastrria and have S-shaped occlusal patterns characteristic of this species. In the sample of P_4 's of *D. smithi* from McKay Reservoir, 16 percent of 24 P_4 's had complete or vestigial parastrriids and paraflexids.

The incisors and most of the ventral region of the premaxillary bone are absent in this specimen. The dorsal surface of the skull is long and relatively flat. Over the orbits the frontal bone forms a broad, flat surface (Fig. 2). The nasal region is straight, with neither the lateral nor dorsal inflation of *Castor canadensis*. A small protuberance exists on the dorsal lip of the fossa for the masseter profundis anterior muscle at the premaxillary-maxillary suture. This protuberance is similar to that in *Castoroides ohioensis*; *Eucastor* has only a slight one and *Castor* lacks one. Frontoparietal crests arise above the orbits and extend posteriorly along the frontal-parietal suture, where they join to form a strong median sagittal crest between the parietal bones. The lambdoidal crests are well developed, extending laterally nearly to the tip of the mastoid processes.

The anterior and posterior temporal foramina are both present on the parietal-squamosal suture and in the same position as in *Eucastor* and *Castoroides*. Approximately ninety percent of the surfaces of the parietal bones are covered with rugosities. *Eucastor* and *Castoroides* also have similar rugosities although not as extensive anteriorly as in this specimen of *Dipoides*. In *Castor*, such rugosities are not as well developed. The dorsal surface of the cranium in *Dipoides* is more inflated than in *Eucastor* but not as inflated as in *Castor*. The occipital plate intersects a plane extended posterior

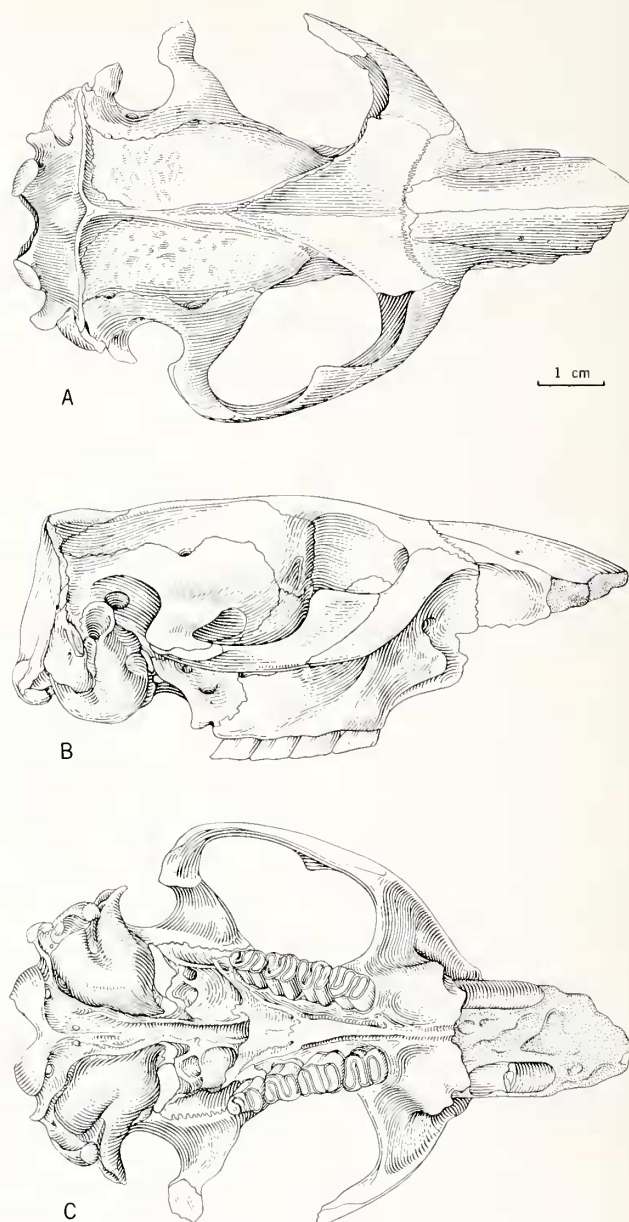


Figure 2. *Dipoides smithi*: Shotwell, 1955, UCMP 113422, McKay Reservoir local fauna, UCMP locality V74163, nearly complete skull lacking the incisor region; A, dorsal view; B, right lateral view; C, ventral view; scale indicated.

from the palate at approximately seventy degrees. By comparison, in *Eucastor*, *Castoroides*, and *Castor*, the occipital plate intersects the same plane at nearly ninety degrees. A small mastoid foramen pierces the mastoid bone slightly lateral to the mastoid-supraoccipital suture. In size and position the mastoid foramen is very similar to that in *Castoroides*. In *Castor*, this foramen is much larger and situated on the mastoid-supraoccipital suture. The occipital condyles appear very similar to those in *Castor* and do not show the transverse flattening of those of *Castoroides*.

Anterior and ventral to the infraorbital foramen there is a very prominent masseter superficialis process (Fig. 3, B). A prominent flange or sheath of bone extends dorsally from the lateral edge of this process, closing off the ventral region of the infraorbital foramen from the masseter lateralis profundus anterior fossa (Fig. 3, B). This flange bends posteriorly toward its dorsal limit and does not extend above the infraorbital foramen. The morphology of the masseteric superficialis process and infraorbital complex in *Dipoides* is nearly identical to that of *Castoroides*. In *Eucastor* the masseteric superficialis process is not well developed, and the structure of the infraorbital region resembles that of *Castor*.

The zygomatic arch is wide, but not to the extreme seen in *Castor* or *Castoroides*. The orbit of *Dipoides* is proportionally larger than in *Castor* and *Castoroides* and appears to be directed more laterally than in *Castor*. The structure of the zygomatic arch and lacrimal region is similar to that in *Castoroides* and *Eucastor* and differs from that in *Castor*. The contribution that the jugal bone makes to the zygomatic arch of *Dipoides*, *Eucastor*, and *Castoroides* is less than in *Castor*. In the former three genera, the jugal-maxilla suture is on the lateral surface of the zygomatic arch as contrasted to *Castor* where this suture is in the lacrimal area. The anterior margin of the orbit is composed of the maxilla, because the jugal does not extend into the lacrimal region. In *Castor*, however, the jugal-maxilla suture extends anteriorly on the dorsal surface of the zygomatic arch, and the jugal meets the lacrimal in the anterior region of the orbit.

Dipoides has a simple lacrimal region in which only the frontal and maxilla meet on the dorsal surface of the skull. The lacrimal bone does not have a dorsal component in this specimen. The structure of the lacrimal region in *Dipoides* and *Castoroides* is similar by having only the two dorsal elements. *Eucastor* differs slightly from *Dipoides* and *Castoroides*, because a small portion of the lacrimal bone is visible on the dorsal surface at the maxillary-frontal suture. *Castor* has a much more complicated dorsal lacrimal area in which the jugal, maxillary, lacrimal, and frontal bones all meet.

The pattern of foramina within the inner orbit of *Dipoides* is very similar to that in *Eucastor* and distinctly different from the pattern in either *Castoroides* or *Castor*. However, the resemblance to *Castoroides* is greater than to *Castor*. The sphenoid foramen is the anterior foramen, piercing the maxillary in an anterior direction. Directly behind the sphenoid foramen is a slightly smaller one that enters the cranium medially. This foramen completely penetrates the cranium as does the presphenoid canal of Olson (1940) (alisphenoid-rotundum foramen of Stirton (1965)). This foramen appears to be an anterior presphenoid canal. Directly above the anterior presphenoid canal on the orbitosphenoid-frontal suture is the ethmoid foramen. Posterior and ventral to the ethmoid foramen is a well-developed optic foramen entirely enclosed in the orbitosphenoid bone. A large posterior presphenoid canal is situated posterior to the optic foramen in a deep sulcus at the anterior end of the sphenoidal fissure. Near the anteroposterior margin of the alisphenoid wing of the internal pterygoid fossa is the masticatory-buccinator

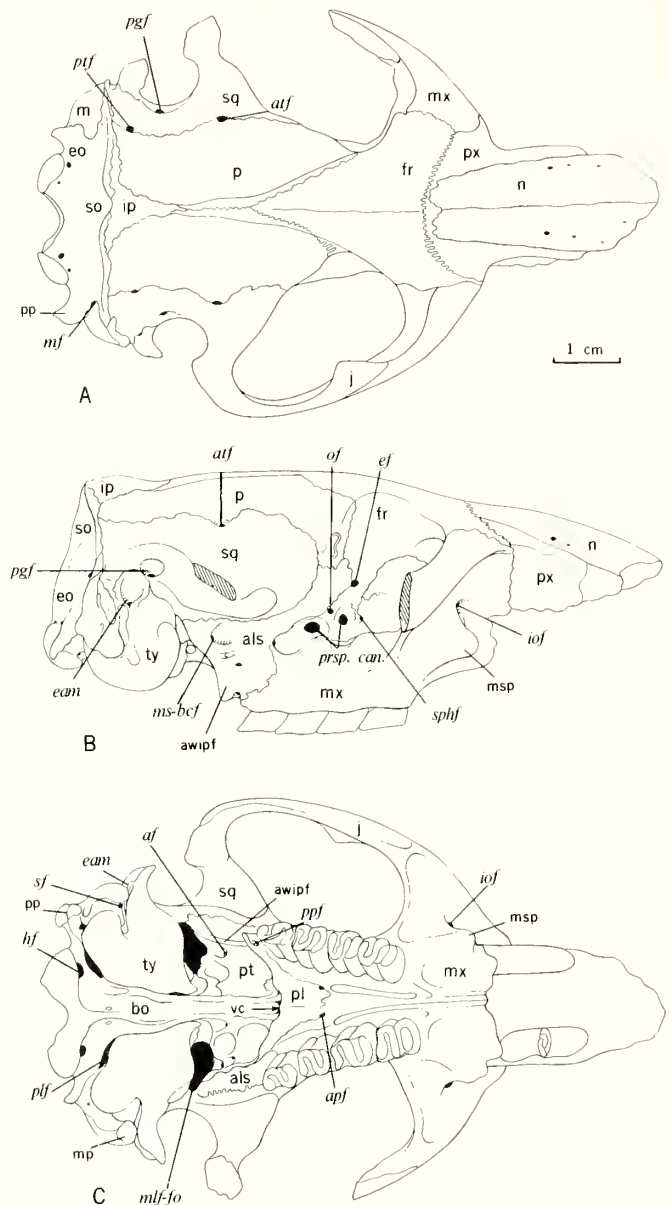


Figure 3. *Dipoides smithi*, Shotwell, 1955, skull with structures labeled, UCMP 113422; A, dorsal view; B, right lateral view; C, ventral view; scale indicated roman type represents bones and structure, italics are foramina. Abbreviations: af, alisphenoid foramen; als, alisphenoid; awipf, anterior palatine foramen; atf, anterior temporal foramen; awipf, alisphenoid wing of internal pterygoid process; bo, basioccipital; eam, external auditory meatus; ef, ethmoid foramen; eo, exoccipital; fr, frontal; hf, hypoglossal foramen; iof, infraorbital foramen; ip, interparietal; j, jugal; m, mastoid; mf, mastoid foramen; mlf-fo, median lacerate foramen-fovea; mp, mastoid process; ms-bcf, masticatory-buccinator foramen; msp, masseteric superficialis process; mx, maxillary; n, nasal; of, optic foramen; p, parietal; pgf, postglenoid foramen; pl, palatine; pp, paroccipital process; prsp. can., presphenoid canal; ps, premaxillary; pt, pterygoid; ptf, posterior temporal foramen; sf, stylomastoid foramen; so, supraoccipital; sphf, sphenoidal foramen; sq, squamosal; ty, tympanic; vc, ventral choana.

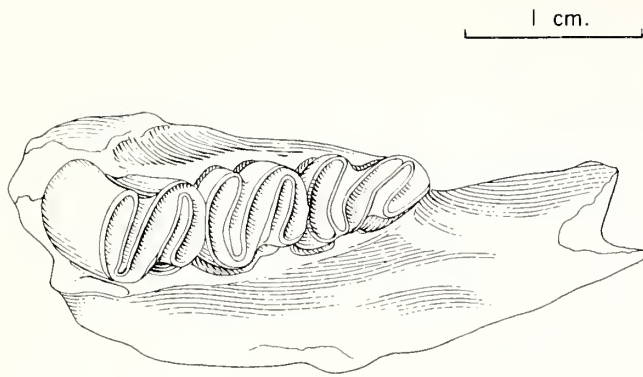


Figure 4. *Dipoides smithi*, UCMP 113433, UCMP V74163, collected near the skull figured in this paper. Left dentary fragment with P_4, M_{1-2} showing normal occlusal wear. This specimen has the more typical P_4 of *D. smithi*, where no paraflexid is present.

foramen. Below the masticatory-buccinator foramen, a portion of the alisphenoid canal is visible, as it passes through the alisphenoid bone. Anteroventral to the alisphenoid canal is a large foramen that appears to enter the pulp cavity of M^3 . The pattern of foramina anterior to and including both presphenoid canals in *Dipoides* is very similar to that in *Eucastor* and *Castor*. *Eucastor* resembles *Dipoides* by having

the multiple presphenoid canals. By contrast, in *Castoroides*, the presphenoid canal is single and proportionally much smaller and more posterior in its position.

Posterior to the presphenoid canal, the morphology of the alisphenoid in *Dipoides* does not resemble that in *Castor* but is very similar to that in *Castoroides*. In *Dipoides* and *Castoroides*, the alisphenoid forms a smooth lateral surface of the sphenoid fissure from the anterior sulcus of the presphenoid canal posterior to the masticatory-buccinator foramen. The masticatory-buccinator foramen is directed posteriorly through the margin of the alisphenoid. In *Castor*, part of the alisphenoid forms a strap-like structure, forming the lateral surface of the alisphenoid canal. The masticatory-buccinator foramen and alisphenoid foramen share a common orifice that is at the posterior end of the straplike structure of the alisphenoid. This common foramen is directed anteriorly, entering directly into the sphenoid fissure. The alisphenoid foramen pierces the broad alisphenoid wing of *Dipoides* and *Castoroides*, and a branch of the trigeminal nerve (V_2) enters the skull through a bone canal enclosed in the alisphenoid wing of the internal pterygoid. *Castor* differs in that the alisphenoid foramen does not pass through the alisphenoid wing, but the trigeminal nerve enters via the alisphenoid foramen. This region of the skull of the specimen of *Eucastor* was not well enough preserved to allow comparison.

The postglenoid foramen is large and nearly equal in size

Table 1. A comparison of cranial characters in *Eucastor* cf. *E. tortus*, CNHM P15787; *Dipoides smithi*, UCMP 113422; *Castoroides ohioensis*, CNHM P3800; and *Castor canadensis*, UCMP 126-158.

Characters	<i>E. cf. E. tortus</i>	<i>D. smithi</i>	<i>C. ohioensis</i>	<i>C. canadensis</i>
Protuberance on dorsal lip of anterior masseteric fossa	slight	slight	well-developed	absent
Temporal foramina present	yes	yes	yes	yes
Rugosities present on parietal bone	slight	well-developed	well-developed	slight
Inflation of cranium	slight	slight	slight	well-developed
Mastoid foramen	small	small	small	large
Masseteric superficialis process well developed	no	yes	yes	yes
Masseteric superficialis process anterior to anterior masseteric fossa	no	yes	yes	no
Lateral vertical flange on infraorbital foramen	yes	no	no	yes
Parallel tooth row on maxillary	yes	no	no	yes
Dorsal choana or invagination on pterygoid or basioccipital bones	no	no	yes	yes
Posterior carotid foramen	absent	absent	present	present
Alisphenoid foramen pierces medial alisphenoid wing of internal pterygoid fossa	not known	yes	yes	no
Jugal extends into lacrimal region	no	no	no	yes
Multiple presphenoid canals	yes	yes	no	yes
Bulla highly inflated	yes	yes	no	yes
Mastoid process extends beyond external auditory meatus	no	no	no	yes

to the external auditory meatus. The external auditory meatus is posterior and ventral to the postglenoid foramen and is appressed posteriorly against the mastoid process and directed laterally. Its anterior lip has the greatest lateral extension. The condition of the postglenoid foramen and external auditory meatus is very similar to that of *Castoroides*. *Castor* and *Eucastor* differ, having a much smaller postglenoid foramen; the meatus has a more dorsolateral orientation, and its ventral lip has the greatest lateral extension. In *Dipoides* and *Castor*, the meatus projects laterally beyond the mastoid process. In *Castoroides*, it does not.

The internal pterygoid fossa is broad, bounded laterally by the alisphenoid wing and medially by the palatal wing of the pterygoid, which is a septum supporting the hamular process. The alisphenoid foramen is present just anterior to the conjoined median lacerate foramen and foramen ovale on the alisphenoid wing of the internal pterygoid fossa (Fig. 3, C). The surface of the pterygoid fossa has depressions. The ventral choana is triangular in outline, bounded laterally by the palatal wings of the pterygoid. In *Castoroides* the outline of the ventral choana is similar to that of *Dipoides*, but in *Castor* it is nearly circular.

There is a rugosity on the anterior median border of the bulla, resembling that of *Castor*, where the hamular process meets the tympanic. In *Castor* these rugosities extend farther posteriorly, so it seems probable that the hamular processes of *Dipoides* were not as long as in *Castor*. The overall structure of the internal pterygoid fossa in *Dipoides* resembles that in *Castoroides*, in which the alisphenoid wing of the internal pterygoid fossa is expanded, and the alisphenoid foramen enters the skull through the medial surface of the alisphenoid. This region of the skull of *Eucastor* was not preserved well enough to allow comparison.

Dipoides does not possess the dorsal choana (mesopterygoid fossa) of *Castoroides* (see Stirton, 1965). This fossa is unique to *Castoroides*. *Castor* does have a shallow invagination in the basioccipital, but this invagination is posterior to the mesopterygoid fossa of *Castoroides*.

A small anterior carotid foramen in *Dipoides* pierces the lateral margin of the basisphenoid anterior to the medial extension of the bulla. It is similar in position to that of *Castor*. In *Dipoides* and *Eucastor*, the posterior carotid foramen is not visible along the medial margin of the bulla anterior to the posterior lacerate foramen as it is in *Castor* and *Castoroides*. A large posterior lacerate foramen is present along the posteromedial border of the bulla. Directly posterior to the posterior lacerate is a large hypoglossal foramen. A small stylomastoid foramen is present, wedged between the base of the mastoid process and the bony tube of the tympanic leading to the external auditory meatus. The paroccipital process extends posteriorly almost as far as do the occipital condyles (see Table 1). The very tip of the paroccipital process is hooked ventromedially.

The bullae are very inflated. Their ventral extension does not reach as far ventrally as the greatest depth of the skull at the tooth row (see Fig. 2, B; Table 2). In *Castor*, the bulla, though exhibiting no greater inflation, extends ventrally to a

Table 2. Measurements of cranial and dental characters of *Dipoides smithi*, UCMP 113422 (in millimeters).

Posterior margin lambdoidal crest to anterior tip of nasals	90.5*
Dorsal width of rostrum anterior to zygomatic arch	17.0
Least width between orbital fossae	14.7
Greatest width between external auditory meatus	45.7
Greatest width between mastoid processes	23.3
Greatest width of zygomatic arches	64.9
Greatest width between masseteric superficialis processes	23.3
Length from dorsal margin of foramen magnum to greatest height of occiput	15.2
Depth of skull between dorsal surface of skull and occlusal surface of M ²	36.8
Depth of skull between sagittal crest and bulla	30.6
Least width of palate between P ⁴ 's	5.2
Least width of palate between M ³ 's	14.4
Length from anterior border of P ⁴ to posterior border of M ³	21.9
Length of occlusal surface of P ⁴	5.8
Width of occlusal surface of P ⁴	5.5
Length of occlusal surface of M ¹	4.9
Width of occlusal surface of M ¹	4.5
Length of occlusal surface of M ²	5.0
Width of occlusal surface of M ²	4.4
Length of occlusal surface of M ³	5.1
Width of occlusal surface of M ³	3.8

* Approximate.

level in line with the tooth row, which is considerably more ventral than in *Dipoides*, *Eucastor*, or *Castoroides*.

In ventral view, the skull of *Dipoides* closely resembles those of *Eucastor* and *Castor* in general outline. The incisors form a crescentic arc that terminates above P⁴. The dilator naris fossa is deep in *Dipoides*, with a well-developed, grooved median ridge present on the maxilla. In *Eucastor*, the dilator naris fossa is deep, as in *Dipoides*; however, in the former, the maxilla slopes steeply toward the maxillary-premaxillary suture, and in the latter a relatively flat platform is present. The masseteric superficialis process of *Dipoides* and *Castoroides* is posterior to the anterior flaring of the maxillary. The cheek tooth row diverges posteriorly from the midline of the skull. *Castoroides* has a similar appearance with closely placed P⁴'s and widely separated M³'s; whereas in *Eucastor* and *Castor*, the cheek tooth rows are nearly parallel. The tooth wear in *Dipoides* forms a flat transverse plane differing from that in *Castor* wherein the upper tooth surface is concave with the labial margin having greater elevation than the lingual edge. There are two nearly parallel medial grooves that run from the premaxillary-maxillary suture posterior to M¹. These grooves resemble those in *Eucastor* and *Castor*,

though in *Dipoides* they are deeper. The anterior palatine foramina are present on the suture between the M^2 's. The posterior palatine foramen is situated directly posterior to M^3 . A ridge is present posterior to the posterior palatine foramen forming the posterolateral margin of the palate. The posterior margin of the palate forming the roof of the mouth of *Dipoides* describes a smooth concave margin. *Eucastor* differs markedly from this condition in having an invagination in the palatine bone that extends anteriorly to the anterior margin of M^3 . *Castor* and *Castoroides* resemble *Dipoides* in this feature.

DISCUSSION

A detailed examination of the cranial morphology of *Dipoides smithi* reveals close similarities to *Eucastor* cf. *E. tortus* and *Castoroides ohioensis*. The similarities in the positions of the foramina in the orbital region and basicranium and in the bone development of the skull in these three species indicate a close phyletic relationship supporting Stirton's (1935) conclusions based on dental morphology. The similarities of the skull in *Dipoides*, *Eucastor*, and *Castoroides* are (1) the relationship of bones of the lacrimal region; (2) the arrangement of foramina in the basicranium and interorbital region; and (3) the development of the alisphenoid wing of the internal pterygoid fossa. *Castor* differs markedly from other genera in all three characteristics.

In *Dipoides* and *Castoroides*, the dorsal surface of the lacrimal region is composed of the maxilla, premaxilla, and frontal bones. *Eucastor* has a lacrimal component. The most anterior extension of the jugal does not reach the lacrimal region. The jugal does contribute to this region of the skull in *Castor*, a definite difference from the other mentioned taxa.

In the *Eucastor*, *Dipoides*, *Castoroides* group, *Eucastor* and *Dipoides* differ in the morphology of the infraorbital foramen from *Eucastor* to *Dipoides*. The structure of the infraorbital foramen in *Dipoides* and *Castoroides* is derivable from the condition found in *Eucastor*. The multiple presphenoid canals in *Eucastor*, *Dipoides*, and some specimens of *Castor* appear to be a primitive trait evolved prior to *Eucastor* and retained in *Eucastor*, *Dipoides*, and *Castor* but lost in *Castoroides*.

The nonparallel upper cheek tooth rows of *Dipoides* and *Castoroides* are derived compared with *Eucastor* and *Castor*. Similar nonparallel tooth rows are seen in some South American histricomorph rodents. It is probable that this represents a modification related to a different masticatory adaptation. For example, the South American rodents that exhibit this

type of modification are primarily aquatic forms, with teeth composed of lophs for grinding, very similar to the castorid genera.

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